# Spore Morphology of the Hawaiian Genus Sadleria (Blechnaceae)

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The Blechnaceae is a small family of terrestrial ferns which includes about eight genera. The family is characterized by fronds with elongate sori (discrete or forming coenosori) on a secondary vein which runs parallel to the midvein of the pinna. These sori are protected by introrse indusia which open toward the costae. Most of the genera of Blechnaceae have a circumtropical, Southern Hemisphere distribution.

The genus *Sadleria* Kaulf. is one of three fern genera endemic to the Hawaiian Islands. Nine species have been described in the genus, including *S. cyatheoides* Kaulf., *S. pallida* Hook. & Arn., *S. souleyetiana* (Gaud.) Moore, *S. squarrosa* (Gaud.) Moore, *S. polystichoides* (Brack.) Heller, *S. unisora* (Bak.) Robinson, *S. hillebrandii* Robinson, *S. fauriei* Copel., and *S. rigida* Copel. Past taxonomic treatments have recognized a variety of species. Hillebrand (1888) recognized four: *S. cyatheoides*, *S. pallida*, *S. souleyetiana*, and *S. squarrosa*, the last species with three varieties. Christensen (1925) recognized seven species, including in addition to the above *S. fauriei*, *S. rigida*, and *S. unisora*. Copeland (1947) and Stone (1967) mentioned that six or seven species exist in the genus. A modern treatment of the genus is lacking.

The species of *Sadleria* are found in a variety of ecological habitats, from bare lava flows to wet rain forests. The most common species, *S. cyatheoides*, is among the first invaders of new lava flows, but is found as well in nearly mature *Acacia-Metrosideros-Cibotium* forest. The remaining species are less common; *S. squarrosa*, for example, is restricted to wet, dark banks in upland rain forest.

Morphologically, the genus is much like *Blechnum*. However, in contrast to the usually non-arborescent rhizome and pinnatifid to pinnate fronds of most *Blechnum* species, the rhizome of *Sadleria* is erect and in most species arborescent and the fronds are bipinnatifid to bipinnate.

There is little available literature on spore morphology in *Sadleria*. Previous studies dealing only with spore size and shape include those by Skottsberg (1942), Selling (1946), Carlquist (1966), and Holbrook-Walker and Lloyd (1973). The following study was undertaken to document more fully spore morphology in this unusual genus, utilizing the scanning electron microscope, to see if this feature could provide insights into the taxonomic relationships of the species.

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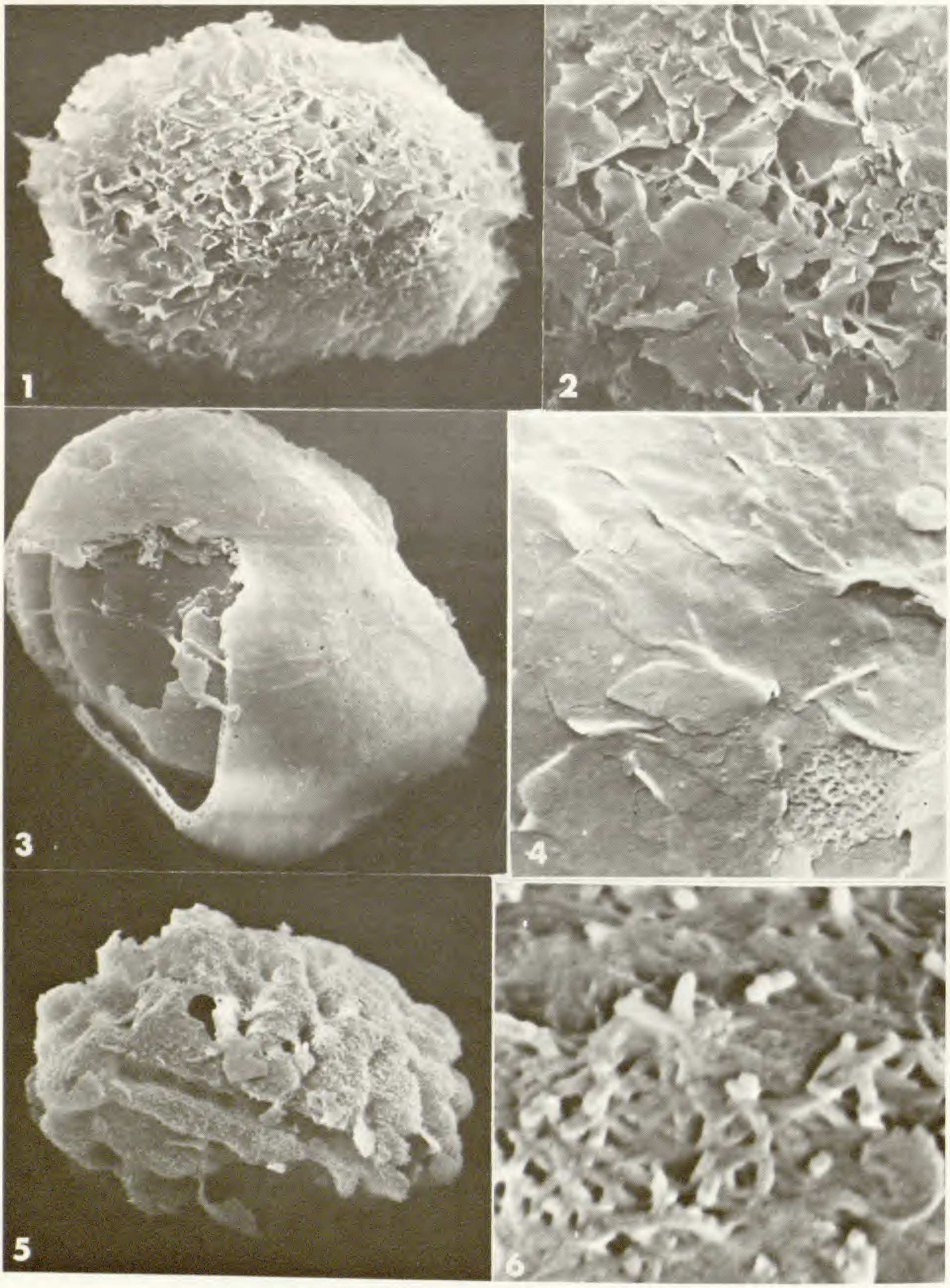



*Sadleria* spores. FIG. 1. *S. hillebrandii, St. John et al. 18447* (MICH), × 1200. FIG. 2. *S. hillebrandii*, surface view, *St. John et al. 18447* (MICH), × 3000. FIG. 3. *S. cyatheoides*, showing broken, multilayered perispore, *Degener 18502* (GH), × 1200. FIG. 4. *S. cyatheoides*, surface view, *Degener 18502* (GH), × 5000. FIG. 5. *S. souleyetiana, St. John 24727* (MICH), × 1100. FIG. 6. *S. souleyetiana*, surface view, *St. John 24727* (MICH), × 6000.

## MATERIALS AND METHODS

Spores were obtained from herbarium specimens of most taxa of *Sadleria*. Untreated spores were mounted on specimen stubs with double-stick tape, coated with gold approximately 10 nm thick, and observed at 20 kv accelerating voltage with a Hitachi HHS-2R scanning electron microscope. Spore sizes were obtained from spores mounted in diaphane and observed with light microscopy. The voucher specimens are:

**S. cyatheoides:** Hawaii: *St. John & Catto 18423* (MICH). Lanai: *St. John & Eames 18752* (MICH). Maui: *Degener 18502* (GH). Oahu: *Copeland s. n.* (MICH), *Fosberg 13309* (MICH).

**S. hillebrandii:** Hawaii: *St. John et al. 18447* (MICH). Maui: *Bonsey s. n.* 13 Aug 1951 (MICH).

**? S. cyatheoides × hillebrandii:** Hawaii: *Degener 18494y* (GH).

**S. pallida:** Oahu: *Degener 10329* (MICH), *Fosberg 13665* (MICH).

**S. souleyetiana:** Maui: *St. John 24725, 24727* (MICH).

**S. squarrosa:** Lanai: *Munro 940* (NY). Molokai: *Crosby & Anderson 1696* (MICH). Oahu: *Grether & Wagner 3924* (US), *Wagner 5756* (MICH).

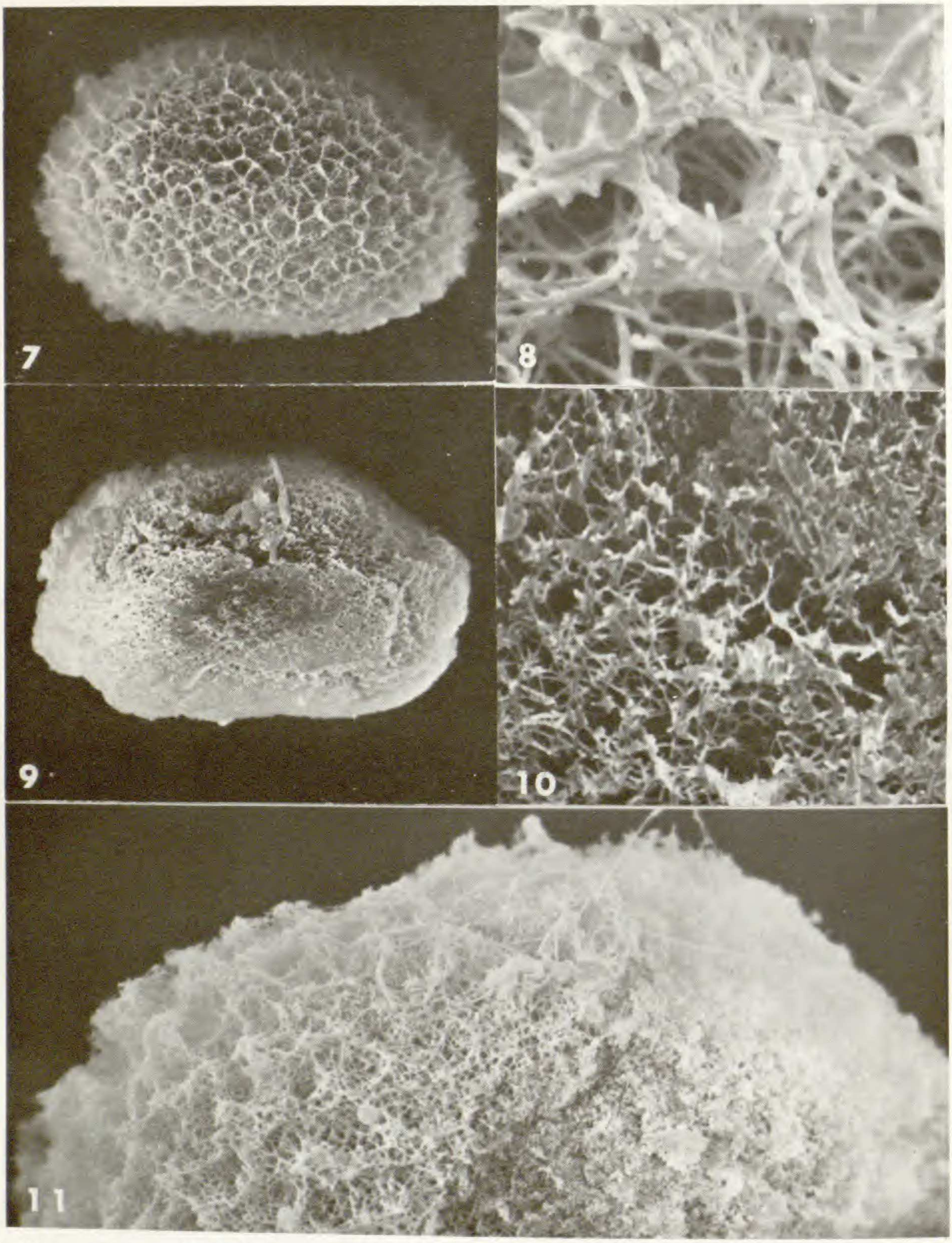
**S. unisora:** Kauai: *Heller 2863* (GH).

## RESULTS

All *Sadleria* spores are bilateral, monolete, somewhat concave-convex in lateral view, and ovate in polar view. The external spore wall appears to be composed of several distinct layers. Light microscopy and scanning electron microscope studies indicate that the innermost layer in all species is smooth and without ornamentation and probably represents the exospore (*Figs. 3* and *14*). On top of this innermost layer are found one, two, or possibly three additional layers of spore wall, which in most species are loosely attached and easily separated from the exospore (*Figs. 3* and *14*). Since the outer layers are easily fractured and are not tightly affixed to the inner exospore, it is most likely that they represent a perispore, although it has not been possible to demonstrate that they are deposited from without the spore. However, in this paper the innermost smooth layer will be referred to as the exospore and the outer loosely attached layers as the perispore. Spore sizes without perispore in *S. cyatheoides*, *S. pallida*, *S. hillebrandii*, and *S. souleyetiana* are similar: 42.0–70.0 (mean = 53.5) $\mu$m long and 26.0–45.0 (mean = 35.4) $\mu$m wide. Spores of *S. squarrosa* and *S. unisora* are significantly larger, however: 58.0–81.0 (mean = 67.5) $\mu$m long and 37.0–56.0 (mean = 45.2) $\mu$m wide.

Spores of *S. hillebrandii* are illustrated in *Figs. 1, 2,* and *13*. The exospore surface is smooth. The perispore appears to consist of a single layer; however, some spores possess what appear to be remnants of an inner layer similar to that of spores of *S. cyatheoides*. The perispores are 2.4–4.4 (7.5) $\mu$m thick and are multitiered as in *S. cyatheoides* (*Fig. 13*). Generally, the surface of the perispore appears to be composed of a series of thin, irregularly sized and shaped plates. This surface pattern overlaps a substructure of small, crowded, irregularly oriented rods, seen in cross-section in *Fig. 13*. The inner surface of the perispore is minutely roughened. The spores of *S. pallida* that were examined were found to be similar in nearly all respects to those of *S. hillebrandii*.

Spores of *S. cyatheoides* are illustrated in *Figs. 3, 4,* and *12*. The exospore surface is smooth (*Fig. 3*). The perispore consists of at least two different lami-




*Sadleria* spores. FIG. 7. *S. unisora, Heller 2863* (GH), × 850. FIG. 8. *S. unisora*, surface view, *Heller 2863* (GH), × 8000. FIG. 9. *S. squarrosa, Grether & Wagner 3924* (US), × 1000. FIG. 10. *S. squarrosa*, surface view, *Grether & Wagner 3924* (US), × 5000. FIG. 11. *S. squarrosa*, surface view, *Munro 940* (NY), × 1200.

nated layers, an inner layer 0.5-1.0 $\mu$m thick, closely appressed to the exospore, and an outer layer. Light microscopy indicates that the total perispore thickness can be up to 10 $\mu$m. The outer surface of the outer layer is more or less smooth, with widely scattered and irregular perforations. An irregular deposition pattern with occasional areas showing the underlying rod pattern can be seen in *Fig. 4*. Connecting the outer and inner surfaces is a series of vertical rods (*Fig. 12*). The inner surface of the outer perispore layer appears to be smooth. The inner layer of perispore is thin and roughened on the external surface (*Fig. 12*). In some spores there is evidence that a third perispore layer exists, internal to the above two layers and overlying the exospore. This layer appears to be very membraneous and less ornamented than the layers above.

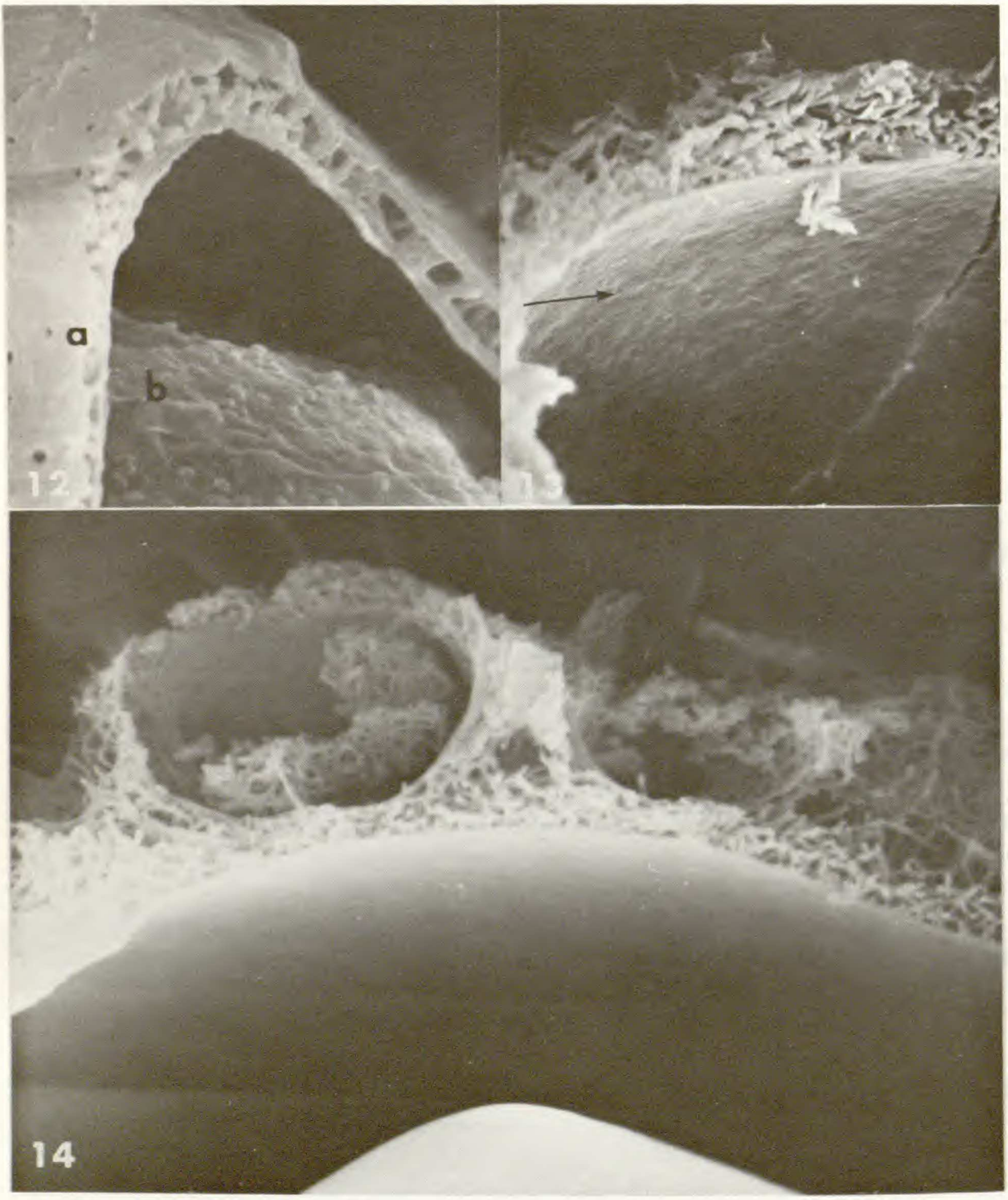
Spores of *S. souleyetiana* are illustrated in *Figs. 5*, *6*, and *14*. The exospore is smooth. The perispore in surface view is highly irregular and tuberculate (*Fig. 5*). The external surface is composed of an irregular and incomplete matrix, through which project numerous, irregularly oriented rods (*Fig. 6*). In some specimens, the matrix is nearly lacking. In cross-section, the perispore is seen to be composed of a single layer, with each tubercle enclosing a large lumen (*Fig. 14*). The interior of the perispore is composed of densely packed irregularly oriented and anastomosing rods. The outer surface of the perispore is variable in different spores. In some spores, the surface consists of irregular deposits between the papillate reticulum (*Fig. 6*); in other spores the deposits are lacking and the surface has a reticulate, areolate-papillate pattern. The perispores are 2.5-5.2 (13.3) $\mu$m thick.

Spores of *S. squarrosa* are illustrated in *Figs. 9-11*. They are more variable in surface pattern than are those of the other species investigated here. The perispore is apparently more tightly affixed to the exospore, as fractured walls were not observed. In the spores of some plants, the perispore is constructed of irregularly sized and shaped anastomosing rods arranged in a reticulum (*Fig. 11*). Spores of *S. unisora* are similar (*Figs. 7, 8*). In other plants, the reticulate pattern of rods and lumina is more minute and difficult to see (*Figs. 9, 10*). Frequently, there are regular deposits of matrix between rods and overlying much of the surface.

Spores from freshly collected specimens of *S. squarrosa* are brownish, but in much of the herbarium material examined the spores appear white, indicating perhaps that some change has occurred in the surface structure or that the material has been bleached out. Hillebrand (1888) indicated that spores of this species were pale, ". . . at first enveloped by a dense layer of soft clavate papillae, which disappear with age, leaving only a rough surface." Fresh spores have not been examined under the scanning electron microscope in this study.

## DISCUSSION

Details of the spore wall that have been discovered using the scanning electron microscope have provided important features which may be used taxonomically to help delimit taxa in *Sadleria*. Four perispore types are present and correspond to *S. hillebrandii*, *S. cyatheoides*, *S. souleyetiana*, and *S. squarrosa*. The spores of *S. pallida* are almost identical to those of *S. hillebrandii*; although the former species is recognizable on other morphological grounds (Degener & Degener,




*Sadleria* spores. FIG. 12. *S. cyatheoides*, cross-section of outer perispore (a) and surface of inner perispore layer (b), *Degener 18502* (GH), × 6300. FIG. 13. *S. hillebrandii*, cross-section of perispore (arrow indicates inner surface), *St. John et al. 18447* (MICH), × 5000. FIG. 14. *S. souleyetiana*, cross-section of perispore, *St. John 24727* (MICH), × 5000.

1974), spore structure indicates a very close relationship to *S. hillebrandii*. Spores of *S. unisora* are nearly identical to spores of some plants of *S. squarrosa*, reinforcing the hypothesis that *S. unisora* is at best only an isolated form of *S. squarrosa*. The morphological features of *S. squarrosa* make it one of the most distinct and easily characterized species in the genus. The spore variation in this species may be due to ontogenetic processes or may indicate divergence in various populations.

Spore diversity in *Sadleria* could lead to a hypothesis that the genus is polyphyletic. However, the spores do have several features in common: a perispore which is composed of small rods which are arranged either in a regular reticulations (in *S. squarrosa* and *S. unisora*) or are more irregularly arranged (in the remaining taxa). The basic difference between spores, with the exception of the laminate perispore of *S. cyatheoides*, is the outer surface pattern of the perispore itself. The multi-layered perispore of *S. cyatheoides* is apparently unique to the genus, although fractured spores of *S. squarrosa* have not been observed.

It can be hypothesized that the basic spore type in the genus is that of *S. cyatheoides*. From this type, by loss of the inner perispore layer and by progressive loss of outer surface deposits, the surface pattern of *S. squarrosa* spores has been produced.

Investigation of spores from plants thought by Degener (pers. comm.) to be hybrids between *S. cyatheoides* and *S. hillebrandii* reveals perispore features which are intermediate between the two species. The outer perispore surface of individual spores exhibits both the irregular plates of *S. hillebrandii*, as well as the smooth surface of *S. cyatheoides* spores, thus supporting Degener's conclusions.

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